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Distribution patterns of stream grazers and relationships between grazers and periphyton at multiple spatial scales

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Abstract. We examined the relationships between the distribution of dominant herbivorous insect grazers (*Glossosoma* larvae), environmental factors (current velocity, water depth, periphyton biomass), and grazer–periphyton interactions at multiple spatial scales (microhabitat, riffle, reach) in a stream. We used multiple regression models to explain densities of *Glossosoma* larvae at each spatial scale in terms of the environmental factors. All r^2-values were significantly higher at the riffle than at the microhabitat or reach scales. Thus, the riffle scale provided better predictions of *Glossosoma* larval density than did the microhabitat (smaller) and reach (larger) scales. The r^2-values of exponential regressions between grazer densities and periphyton biomass were lower at the microhabitat than at the riffle or reach scales. These results indicate that the patterns of relationships between the insect grazers and periphyton were detected more clearly at larger than at smaller scales.

Key words: spatial scales, caddisfly, top-down, microhabitat, riffle, reach.

Scaling is a central concept and problem in ecology (Schneider 2001). Our understanding of ecological processes can depend on the scale at which they were measured. Therefore, thought should be given to the appropriate scale at which to measure species distributions, interspecific interactions, and community and ecosystem processes (e.g., Levin 1992, Wiens 2002). In stream ecosystems, ecological and geomorphological features often are used to define hierarchies of spatial scales. One commonly used spatial hierarchy includes (in ascending order) microhabitats, riffles, reaches, segments, and catchments (Woodward and Hildrew 2002).

In general, the variables most likely to influence stream macroinvertebrates operate at scales below segments (*habitat scale*) (Johnson and Goedkoop 2002, Townsend et al. 2003, Johnson et al. 2004). These variables include water movement, bed morphology, and periphyton productivity (e.g., Townsend et al. 2003, Johnson et al. 2004, Katano et al. 2007). For example, caddisflies and mayflies often are the dominant grazers in stream macroinvertebrate assemblages (Allan 1995, Feminella and Hawkins 1995). The distribution of these grazers is influenced by physical habitat features, such as flow regime, and by the condition of the periphyton mat, which provides food resources (Feminella and Hawkins 1995, Katano et al. 2005). However, our understanding of the relationships between grazer distributions and flow and condition of the periphyton mat could differ depending on the spatial scale at which measurements were made.

Top-down (consumer-driven) and bottom-up (resource-driven) effects usually are studied at small spatial scales with consumer-exclusion methods (Hunter 2001). Several studies have applied a multiple-scale approach to herbivore–producer interactions (e.g., Kohler and Wiley 1997, Taylor et al. 2002), but few studies have compared herbivore–producer inter-

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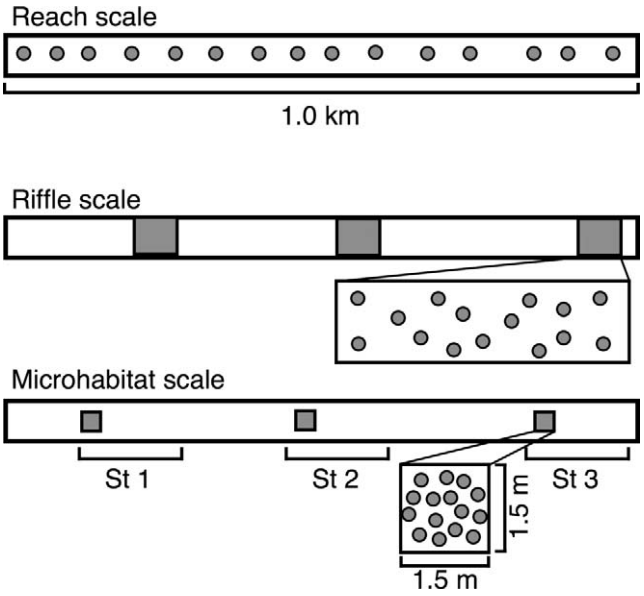

FIG. 1. Sampling design at 3 spatial scales. Gray circles represent individual cobbles.

actions across different scales in the field. Wellnitz et al. (2001) found that the effects of environmental variables on distributions of and interactions between insect grazers and periphyton differed among 3 spatial scales (microhabitat, riffle, and reach). Thus, the spatial scale at which a study is conducted is important. However, the appropriate scale to use is not always clear.

We addressed 2 main questions: 1) At which spatial scale should grazer distributions be studied in streams? 2) At which spatial scale should grazer–periphyton interactions be studied in streams? We hypothesized that grazer–periphyton interactions would be more apparent at small than at large spatial scales because most studies have detected significant effects of herbivory at small experimental scales (e.g., Hart 1987, Hill and Knight 1987, 1988, Kuhara et al. 2000, 2001). We quantified grazers, periphyton, and environmental factors on individual cobbles (grain = 1 cobble) at 3 spatial scales (microhabitat, riffle, reach) to determine the optimal spatial scale at which to measure distributions of and interactions between grazers and periphyton.

Methods

Study area

We conducted our study in a 7th-order, 1.0-km reach of the Hirose River in Sendai, northern Japan (lat 38°15′N, long 140°50′E; stream order calculated from a 1:25,000 map of the area). Watershed area was ~360 km^2. The reach consisted of a series of riffles and runs with depths ranging from 5 to 40 cm, and the width of the reach was ~25 m. Discharge ranged from 5 to 10 m^3/s in February and March (data from Japanese Ministry of Land and Transport, http://www1.river.go.jp). Current velocity, measured just above the river bottom with a portable current meter (model CR-11WP; Cosumo Riken, Kashihara, Japan) ranged from 18.5 to 44.8 cm/s. The stream bed consisted of cobble and pebbles throughout the study reach. Streamwater nutrient content, streambed morphology, and canopy cover by riparian forests were similar at all sampling locations. Riparian vegetation was dominated by reed (*Phragmites japonica*).

Sampling design

We sampled at 3 spatial scales: reach, riffle, and microhabitat. At each spatial scale, we sampled 15 individual cobbles from the appropriate scale and unit of replication (3 microhabitat quadrats, 3 riffles, or 1 reach) so that the spatial resolution (grain = 1 cobble; 10–30 cm in diameter) of our sampling scheme was the same at each spatial scale (Fig. 1). At the reach scale, we selected 1 cobble from each of 15 riffles (15–30 m in length) that had homogeneous stream flow from our 1.0-km study section. We selected each cobble from the approximate center of each riffle according to the method of Wellnitz et al. (2001). At the riffle scale, we sampled 15 cobbles from each of 3 riffles (St 1, St 2, St 3; 15–30 m in length) within the reach by selecting points using a random-walk technique (Wellnitz et al. 2001). At the microhabitat scale, we sampled 15 cobbles randomly from 1.5 × 1.5-m^2 quadrats in the approximate center of each of the 3 riffles used at the riffle scale (St 1, St 2, St 3). A preliminary survey indicated that the quadrat size used was the minimum area required to provide 15 cobbles.

We focused mainly on *Glossosoma* larvae because this genus was the dominant herbivore in the stream. *Glossosoma* spp. made up 95% of the dry mass of all macroinvertebrate grazers. *Goera japonica*, *Epeorus latifolium*, and *Baetis* spp. were also present but had negligible biomass (<5%). We collected the samples during 2 sampling periods (12–15 February and 5–9 March) because the river is regulated by a dam, and the discharge is relatively stable in late winter.

On each sampling date, we estimated the density of *Glossosoma* larvae, periphyton ash-free dry mass (AFDM), cobble surface area, water depth, and current velocity over cobbles. We chose water depth, current velocity, and periphyton AFDM as environmental factors of interest on the basis of results from Wellnitz et al. (2001), who also estimated the distribution of

Glossosomatidae species in a stream at multiple spatial scales. We used AFDM rather than chlorophyll *a* to estimate periphyton biomass because AFDM is a more sensitive indicator of grazer effects than is chlorophyll *a* (Feminella and Hawkins 1995).

Sample processing

We processed all cobbles in the same manner regardless of the scale at which they were sampled. Before removing a cobble from the stream bed, we measured current velocity immediately above the cobble with a portable current meter (model CR-11WP; Cosumo Riken, Kashihara, Japan), and we measured water depth with a ruler. We placed a 250-μm-mesh Surber net downstream of the cobble, gently moved the cobble into the net, and transferred the cobble into a pan. We used a pair of forceps to remove *Glossosoma* larvae and other macroinvertebrates from the cobble surface in the field. We preserved larvae in 5% formalin for later counting in the laboratory.

We scrubbed the periphyton mat from the cobble surface using a brush. We filtered the resulting slurry through a precombusted (500°C, 2 h) Whatman GF/C glass-fiber filter (Whatman International Ltd., Maidstone, UK) to collect the periphyton. We dried the filter at 60°C for 24 h, weighed it, combusted it at 500°C for 2 h in a muffle furnace, and reweighed it. We calculated periphyton AFDM as the difference between the masses before and after combustion. We quantified the surface area of the cobble by wrapping the cobble in aluminum foil and trimming off the excess material (Steinman and Lamberti 1996). We dried the foil at 60°C, weighed it, and used a mass–area relationship to determine the surface area of the cobble. *Glossosoma* density and periphyton AFDM were expressed as individuals (ind.)/100 cm^2 and mg/100 cm^2 of cobble surface area, respectively.

Statistical analysis

We used the statistical software R (version 2.5.0; R Development Core Team 2007) for all analyses. We used a multiple regression model with the environmental factors (current velocity, water depth, and periphyton AFDM) to predict *Glossosoma* larval distribution for each month. The model was

$$\textit{Glossosoma}\ \text{density}(Y) = b_0 + b_c X_c + b_d X_d + b_a X_a,$$

where b_0 is a regression constant, and b_c, b_d, and b_a are the regression coefficients for current velocity (X_c), water depth (X_d), and periphyton AFDM (X_a), respectively. To normalize the data, the values for environmental factors (current velocity, water depth, and periphyton AFDM) were $\log_{10}(x + 1)$-transformed prior to regression analysis.

We calculated regression coefficients, partial correlation *r*-values for each variable, r^2-values, and *p*-values for the full models for the data for each month (February, March) at each spatial scale (microhabitat, riffle, reach) and sampling location (St 1, St 2, St 3 at the microhabitat and riffle scales). Thus, we calculated 14 multiple regression models (2 months × [3 sampling locations at the microhabitat scale + 3 sampling locations at the riffle scale + 1 reach]). Each regression was calculated with data from the 15 cobbles collected at the appropriate scale, sampling location (microhabitat and riffle scales), and month (February and March). The effect of month and spatial scale (microhabitat, riffle) on the r^2-values of the multiple regression models was tested using repeated-measures 2-way analysis of variance (rm 2-way ANOVA, month × spatial scale, $n = 3$ sampling locations in each treatment combination). We compared r^2-values for microhabitat- and riffle-scale models with paired *t*-tests ($n = 6$ months × sampling location combinations).

We calculated coefficients of variation (CVs) for current velocity, water depth, periphyton AFDM, and *Glossosoma* density for each spatial scale, month, and sampling location (2 months × [3 sampling locations at the microhabitat scale + 3 sampling locations at the riffle scale + 1 reach]). We tested the effects of month and spatial scale on the CVs of *Glossosoma* density and environmental factors with 2-way ANOVA (month × spatial scale, $n = 3$ sampling locations in each treatment combination).

Many previous studies in stream ecosystems have predicted that interactions between grazers and periphyton should lead to an exponential relationship between $\log_{10}(x)$-transformed periphyton AFDM and grazer density (e.g., Feminella and Hawkins 1995, Poff and Ward 1995). Therefore, we did exponential regressions between $\log_{10}(x)$-transformed periphyton AFDM and *Glossosoma* density for each month (February, March) for each spatial scale, month, and sampling location (2 months × [3 sampling locations at the microhabitat scale + 3 sampling locations at the riffle scale + 1 reach]). Each regression was calculated with data from 15 cobbles collected at the appropriate scale (see *Sampling design* above).The model was

$$\log_{10}(x) - \text{transformed periphyton AFDM}(Y) = \text{a}e^{X},$$

where X was *Glossosoma* density. We tested the effects of month and spatial scale on the r^2-values of the regressions with 2-way ANOVA (month × spatial scale, $n = 3$ sampling locations in each treatment combination).

TABLE 1. Multiple regression models (r-values for the parameters, r^2-values for the full models, and p-values, $n = 15$) used to predict *Glossosoma* larval density at the microhabitat, riffle, and reach spatial scales in February and March. Each model was constructed with data from 15 cobbles sampled at 1 of 3 sampling locations at the microhabitat and riffle scales or 15 cobbles collected across the reach. The model variables are current velocity (current), water depth (depth), and periphyton ash-free dry mass (AFDM). CV = coefficient of variation, $CV_{density}$ = the CV of *Glossosoma* larval density. Values in bold are statistically significant ($p < 0.05$).

Model	Sampling location	$CV_{density}$	Variable	CV (%)	r or r^2	p
February						
Microhabitat	St 1	58.6	Current	42.4	0.017	0.955
			Depth	44.0	0.159	0.605
			AFDM	89.5	−0.314	0.296
			Full model		0.119	0.692
	St 2	39.9	Current	41.8	0.171	0.576
			Depth	49.8	0.285	0.346
			AFDM	75.9	**−0.562**	**0.046**
			Full model		0.346	0.182
	St 3	50.9	Current	43.3	0.370	0.213
			Depth	42.3	0.218	0.475
			AFDM	63.9	−0.167	0.585
			Full model		0.186	0.502
Riffle	St 1	55.7	Current	49.9	**0.639**	**0.019**
			Depth	56.5	0.461	0.113
			AFDM	90.5	−0.385	0.194
			Full model		**0.599**	**0.015**
	St 2	39.9	Current	47.0	0.087	0.779
			Depth	51.2	**0.659**	**0.014**
			AFDM	137.1	−0.184	0.548
			Full model		**0.503**	**0.046**
	St 3	53.8	Current	47.0	0.163	0.594
			Depth	53.3	0.306	0.309
			AFDM	126.7	−0.513	0.073
			Full model		0.367	0.155
Reach		66.1	Current	43.7	0.167	0.645
			Depth	53.7	−0.195	0.589
			AFDM	114.1	−0.464	0.177
March			Full model		0.303	0.384
Microhabitat	St 1	57.2	Current	43.5	0.060	0.845
			Depth	50.8	0.338	0.259
			AFDM	133.2	−0.463	0.112
			Full model		0.248	0.352
	St 2	46.7	Current	42.4	0.120	0.697
			Depth	44.0	0.370	0.213
			AFDM	148.3	−0.509	0.076
			Full model		0.276	0.296
	St 3	70.5	Current	42.3	0.193	0.528
			Depth	44.2	0.142	0.642
			AFDM	92.7	−0.390	0.188
			Full model		0.255	0.337
Riffle	St 1	66.8	Current	47.5	0.125	0.685
			Depth	50.2	0.313	0.298
			AFDM	103.0	**−0.577**	**0.039**
			Full model		**0.525**	**0.036**
	St 2	55.7	Current	49.9	0.636	0.019
			Depth	56.5	0.435	0.138
			AFDM	83.8	−0.336	0.262
			Full model		**0.582**	**0.019**
	St 3	66.1	Current	47.0	0.226	0.457
			Depth	45.2	0.303	0.315
			AFDM	122.2	−0.404	0.171
			Full model		0.299	0.253
Reach		48.5	Current	45.7	−0.224	0.534
			Depth	55.7	−0.126	0.729
			AFDM	90.9	−0.209	0.562
			Full model		0.203	0.588

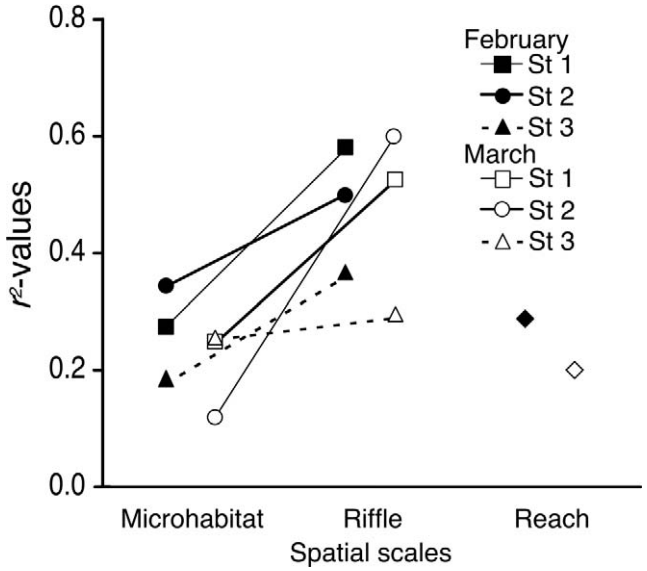

FIG. 2. The r^2-values of multiple regression models used to predict *Glossosoma* larval density in February and March. Each model was constructed with data from 15 cobbles sampled at 1 of 3 spatial scales (microhabitat, riffle, or reach) in 1 of 2 months (February or March). The same riffles (St 1, St 2, St 3) were used for microhabitat- and riffle-scale sampling. r^2-values from microhabitat- and riffle-scale models in the same riffle and month are connected by line segments. The differences between r^2-values connected with line segments were used in a paired *t*-test to determine whether r^2-values differed between the microhabitat and riffle scales.

Results

The CVs of periphyton AFDM were significantly higher than the CVs of current velocity or water depth across all models (2-way ANOVA, $F = 129.7$, $p < 0.001$; Table 1). CVs of water depth and current velocity differed significantly between spatial scales (2-way ANOVA, $F = 6.73$, $p = 0.015$), but not between months (2-way ANOVA, $F = 3.25$, $p = 0.083$). Therefore, the variances of the environmental variables did not affect the comparison of multiple regression models between months. CVs of *Glossosoma* density did not differ significantly between months or between spatial scales (2-way ANOVA; month: $F = 0.805$, $p = 0.396$; spatial scale: $F = 0.356$, $p = 0.567$). Therefore, the variance of *Glossosoma* density did not affect the comparison of multiple regression models between months or spatial scales.

Glossosoma density was negatively related to periphyton AFDM and positively related to current velocity and water depth in all microhabitat- and riffle-scale models, but the relationships between individual environmental variables and *Glossosoma* density generally were not statistically significant (Table 1). Riffle-scale full models explained a significant amount of the variability in *Glossosoma* density at St 1 and St 2 in February and March (Table 1). Neither the February nor March reach-scale full models were statistically significant (Table 1). However, *Glossosoma* density was negatively related to water depth and periphyton AFDM in both models, positively related to current velocity in February, and negatively related to current velocity in March model (Table 1). The relationships between individual environmental variables and *Glossosoma* density were not statistically significant in the reach-scale models. In 9 of 14 models, the highest $|r|$-values were associated with periphyton AFDM.

The r^2-values of the multiple regression models differed significantly among spatial scales but not between months (rm 2-way ANOVA; spatial scale: $F = 7.72$, $p = 0.024$; month: $F = 0.39$, $p = 0.550$; Fig. 2). The month $\times$ spatial scale interaction term was statistically significant ($p = 0.029$). The r^2-values of riffle-scale models were significantly higher than r^2-values of microhabitat-scale models (paired *t*-test, $p = 0.03$). Thus, current velocity, water depth, and periphyton AFDM had greater predictive power at the riffle than at the microhabitat or reach scales.

The r^2-values for exponential regressions at the microhabitat scale in February and March ranged from 0.014 to 0.178 and did not differ among months or sampling locations (ANOVA, $p > 0.05$, $n = 15$ stones/regression; Figs 3A–C, 4A–C), except at St 3 in February (Fig. 3C). Only 1 exponential regression model at the microhabitat scale (February, St 3; Fig. 3C) was statistically significant. The r^2-values at the riffle and reach scales in February and March ranged from 0.144 to 0.332 and differed significantly between spatial scales (February: $p = 0.03$, March: $p = 0.004$, $n = 15$; Figs 3D–G, 4D–G). At the riffle and reach scales, *Glossosoma* larvae significantly reduced periphyton AFDM in both months. The shapes and r^2-values of the exponential regressions of periphyton AFDM on *Glossosoma* density were similar at the riffle and reach scales in both months. Periphyton AFDM and *Glossosoma* densities did not differ among sampling units and months (rm 2-way ANOVA, $p > 0.2$). Therefore, we pooled data across months and sampling locations within spatial scales and recalculated the exponential regressions at each scale (microhabitat: $n = 90$, riffle: $n = 90$, reach: $n = 30$). The r^2-value was higher at the reach than at the microhabitat or riffle scales (Fig. 5A–C).

Discussion

An optimal spatial scale for estimating species distributions, interspecific interactions, and community and ecosystem processes is required when consid-

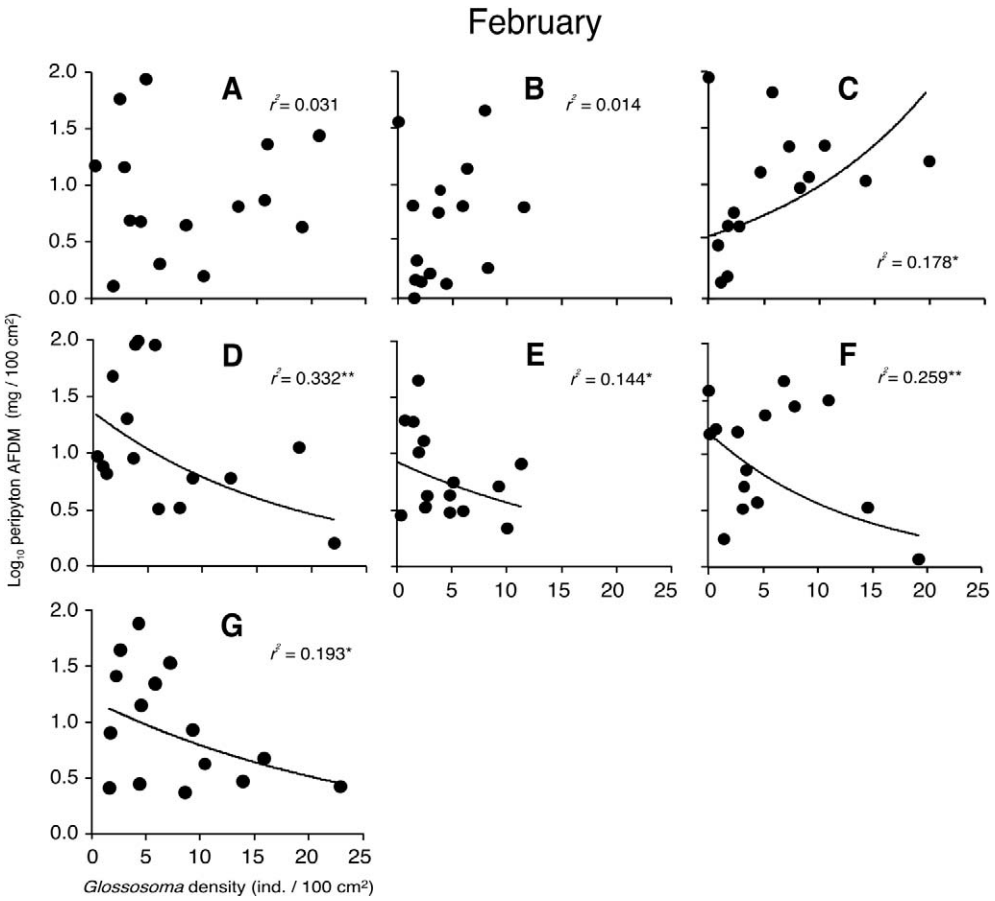

FIG. 3. Relationship between $\log_{10}(x)$-transformed periphyton ash-free dry mass (AFDM) and *Glossosoma* density in microhabitat St 1 (A), St 2 (B), and St 3 (C), riffle St 1 (D), St 2 (E), and St 3 (F), and the entire reach (G) in February. Each exponential regression was constructed with data from 15 cobbles sampled at 1 of 3 sampling locations at the microhabitat and riffle scales or 15 cobbles collected across the reach. See text for details. * = $p < 0.05$, ** = $p < 0.01$.

ering ecological processes that occur at multiple spatial scales (e.g., Levin 1992, Turner et al. 2001, Wiens 2002). We have shown that periphyton AFDM, water depth, and current velocity predicted the distribution of *Glossosoma* larvae better at the riffle scale than at the microhabitat (smaller) or reach (larger) scales. Therefore, our spatial hierarchical approach was useful for assessing the optimal spatial scale at which to predict *Glossosoma* distributions from the environmental variables tested in our study.

In general, habitat variables, such as water movement, substratum, water chemistry, and riparian vegetation, are important descriptors of community composition for stream animals (Johnson et al. 2004). Moreover, these variables are important predictors of stream macroinvertebrate community composition (e.g., Statzner et al. 1988, Richards et al. 1997). Our results suggest that the riffle scale provided the best deterministic power for estimating the distribution of macroinvertebrates. Wellnitz et al. (2001) also suggested that current velocity best predicted Glossosomatidae distribution when sampling was done at the scale of the riffle because of the presence of many cobble-scale habitats and high variation in current velocity at this spatial scale. However, Wellnitz et al. (2001) also showed that 2 grazer species responded differently to environmental variables at the same spatial scale. Thus, the optimal spatial scale at which to predict *Glossosoma* distributions might not be applicable to other species in our study system.

The intrinsic problem for scaling approaches in ecology is that patterns evident at one scale might not be detected at other scales (Allen and Starr 1988, Wiens 1989, Schneider 2001). In stream ecosystems, top-down effects of insect grazers strongly determine periphyton abundance (Feminella and Hawkins 1995). Strong interactions between *Glossosoma* larvae and periphyton have been detected in experimental studies done at small scales (e.g., Hill and Knight 1987, 1988, Kuhara et al. 2000, 2001). We hypothesized that detection of

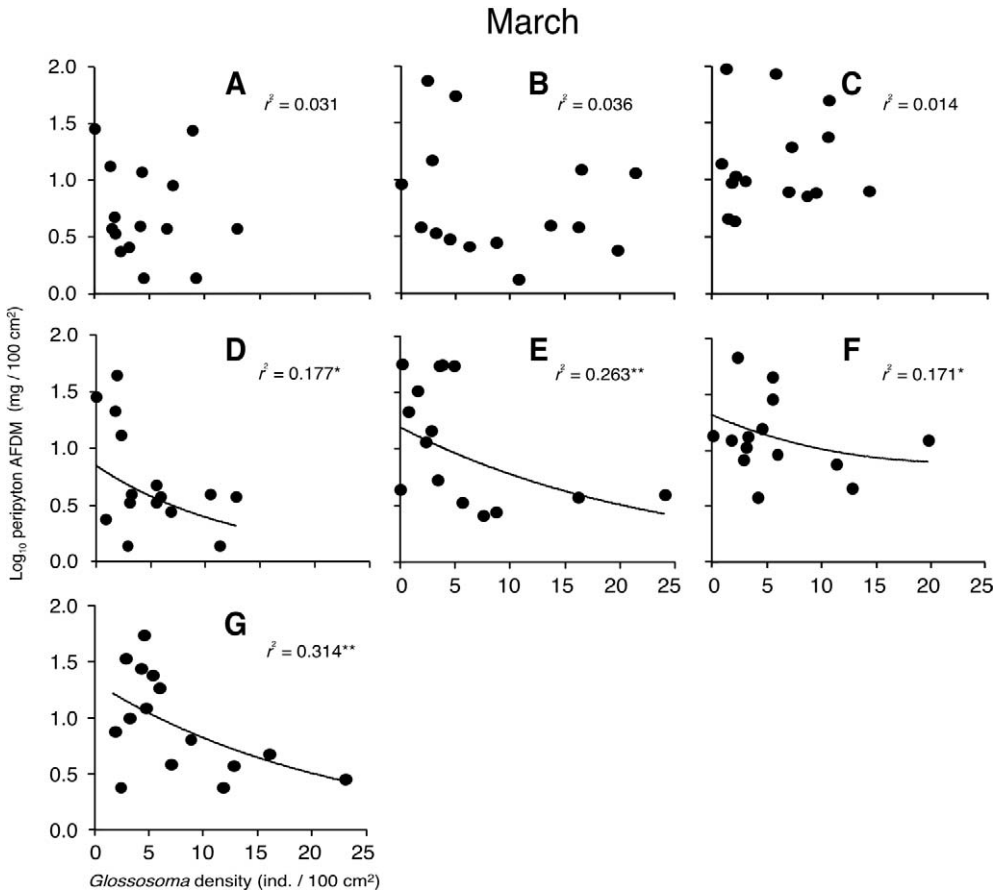

FIG. 4. Relationship between $\log_{10}(x)$-transformed periphyton ash-free dry mass (AFDM) and *Glossosoma* density in microhabitat St 1 (A), St 2 (B), and St 3 (C), riffle St 1 (D), St 2 (E), and St 3 (F), and the entire reach (G) in March. Each exponential regression was constructed with data from 15 cobbles sampled at 1 of 3 sampling locations at the microhabitat and riffle scales or 15 cobbles collected across the reach. See text for details. * = $p < 0.05$, ** = $p < 0.01$.

grazer–periphyton interactions would be better at smaller than at larger spatial scales. However, we observed that the relationship between *Glossosoma* density and periphyton AFDM was clearer at the reach and riffle scales than at the microhabitat scale. Thus, top-down effects of *Glossosoma* on periphyton were more evident at larger than at small scales in our field study.

In enclosed experimental streams, environmental conditions are relatively uniform within the habitat (e.g., Hill and Knight 1988, Kuhara et al. 2000, 2001), and this lack of variability can intensify grazer–periphyton interactions (Feminella and Hawkins 1995). In the field, *Glossosoma* larvae can move among habitat patches with a wider range of environmental conditions and periphyton densities. Many studies have suggested that insect grazers respond positively to habitats with dense periphyton patches (i.e., Hill and Knight 1987, 1988, Doi et al. 2006). Grazer movements can be detected over several days to weeks in riffles or laboratory streams (Lamberti et al. 1987, Hill and Knight 1988, Hart and Robinson 1990, DeNicola and McIntire 1991). Movement of *Glossosoma* larvae in the field is limited to 10 cm/h, and the distance moved does not differ between day and night (Kuhara et al. 2001). Thus, the maximum distance larvae might move is ~2.4 m/d (10 cm/h × 24 h). Drift of *Glossosoma* larvae is intermediate among stream invertebrates (Waters 1962). Thus, *Glossosoma* larvae have the ability to move among microhabitat patches over periods of days. However, their ability to move among riffles or reaches is much smaller than their ability to move among microhabitat patches within riffles. Therefore, differences in *Glossosoma*'s ability to sample cobbles between the small- and larger-scale sampling units might have affected our ability to use environmental variables to predict its distribution at the microhabitat scale and decreased the correspondence between *Glossosoma* density and environmental variables.

In a meta-analysis of grazer–periphyton interactions, field experiments tended in reaches to show stronger effects of grazers on periphyton AFDM than did laboratory experiments (Feminella and Hawkins

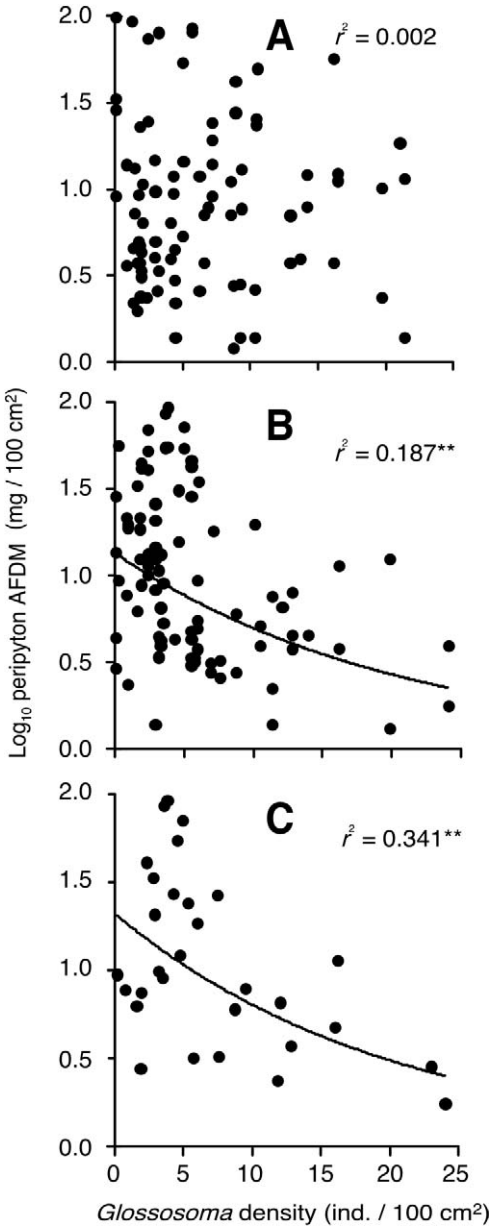

FIG. 5. Relationship between $\log_{10}(x)$-transformed periphyton ash-free dry mass (AFDM) and *Glossosoma* density based on data pooled across months and sampling locations within the microhabitat (A), riffle (B), and reach (C) scales. Exponential regressions at the microhabitat and riffle spatial scales were constructed with data from 90 cobbles, and the exponential regression at the reach spatial scale was constructed with data from 30 cobbles. * = $p < 0.05$, ** = $p < 0.01$.

1995). Results from our study agree. Feminella and Hawkins (1995) suggested that the differences in strengths of the effects were determined by environmental factors, such as temperature, current velocity, and light conditions. In our study, temperature, current velocity, and light conditions did not differ among microhabitats or riffles within the 1-km reach. Thus, variability in environmental factors within or among spatial scales did not affect our ability to detect grazer distribution and grazer–periphyton interactions.

We found a positive correlation between *Glossosoma* density and log-transformed periphyton AFDM at microhabitat St 3 in February (Fig. 3C). This phenomenon is not generally observed (Feminella and Hawkins 1995). Cobbles with high densities of *Glossosoma* and periphyton AFDM are relatively rare. However, these rare cobbles were more likely to be sampled at the microhabitat scale than at larger scales because sampling intensity was much greater in quadrats than in riffles or reaches (i.e., nearly all cobbles in a quadrat vs 1 cobble per reach). Benthic organisms in streams have patchy distributions (Pringle et al. 1988, Allan 1995), and stochastic factors play an important role in determining whether a patch will be colonized (Townsend 1989, Hart 1992). Therefore, the ability to detect significant grazer–periphyton interactions might vary with scale because of differences associated with sampling probabilities at different scales.

Our results indicate that the riffle scale is the most appropriate spatial scale to use when estimating the distribution of caddisfly grazers with low mobility and grazer–periphyton interactions. However, caddisflies and mayflies differ in their responses to current velocity (Wellnitz et al. 2001), and such differences might cause the optimal sampling scale to differ among types of grazers. Moreover, responses might be different in other kinds of streams (i.e., low current and low periphyton abundance), with the consequence that the optimal sampling scale might differ from that observed in our study system. Thus, the appropriate spatial scales for estimating the distributions and interspecific interactions of stream invertebrates must be considered explicitly in stream ecosystems.

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Literature Cited

ALLAN, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, New York.

ALLEN, T. F. H., AND T. B. STARR. 1988. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois.

DENICOLA, D. M., AND C. D. MCINTIRE. 1991. Effects of hydraulic refuge and irradiance on grazer–periphyton interactions in laboratory streams. Journal of the North American Benthological Society 10:251–262.

DOI, H., I. KATANO, AND E. KIKUCHI. 2006. The use of algal-mat habitat by aquatic insect grazers: effects of microalgal cue. Basic and Applied Ecology 7:153–158.

FEMINELLA, J. W., AND C. P. HAWKINS. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of the North American Benthological Society 14:465–509.

HART, D. D. 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia (Berlin) 73:41–47.

HART, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia (Berlin) 91:220–228.

HART, D. D., AND C. T. ROBINSON. 1990. Resource limitation in a stream community: phosphorus enrichment effects on periphyton and grazers. Ecology 71:1494–1502.

HILL, W. R., AND A. W. KNIGHT. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955–1965.

HILL, W. R., AND A. W. KNIGHT. 1988. Concurrent grazing effects of two stream insects on periphyton. Limnology and Oceanography 33:15–26.

HUNTER, M. D. 2001. Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. Basic and Applied Ecology 2:295–309.

JOHNSON, R. K., AND W. GOEDKOOP. 2002. Littoral macroinvertebrate communities: spatial scale and ecological relationships. Freshwater Biology 47:1840–1854.

JOHNSON, R. K., W. GOEDKOOP, AND L. SANDIN. 2004. Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. Freshwater Biology 49:1179–1194.

KATANO, I., H. DOI, A. HOUKI, Y. ISOBE, AND T. OISHI. 2007. Changes in periphyton abundance and community structure with the dispersal of a caddisfly grazer, *Micrasema quadriloba*. Limnology 8:219–226.

KATANO, I., H. MITSUHASHI, Y. ISOBE, H. SATO, AND T. OISHI. 2005. Reach-scale distribution dynamics of a grazing stream insect, *Micrasema quadriloba* Martynov (Brachycentridae, Trichoptera), in relation to current velocity and periphyton abundance. Zoological Science 22:853–860.

KOHLER, S. L., AND M. J. WILEY. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. Ecology 78:2164–2176.

KUHARA, N., S. NAKANO, AND H. MIYASAKA. 2000. Flow rate mediates the competitive influence of a grazing caddisfly on mayflies. Ecological Research 15:145–152.

KUHARA, N., S. NAKANO, AND H. MIYASAKA. 2001. Alterations in the grazing activities of cased caddisfly larvae in response to variations in predation risk and resource level. Ecological Research 16:705–714.

LAMBERTI, G. A., J. W. FEMINELLA, AND V. H. RESH. 1987. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia (Berlin) 73:75–81.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

POFF, N. L., AND J. V. WARD. 1995. Herbivory under different flow regimes: a field experiment and test of a model with a benthic stream insect. Oikos 71:179–188.

PRINGLE, C. M., R. J. NAIMAN, G. BRETSCHKO, J. R. KARR, M. W. OSWOOD, J. R. WEBSTER, R. L. WELCOMME, AND M. J. WINTERBOURN. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503–524.

R DEVELOPMENT CORE TEAM. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RICHARDS, C., R. J. HARO, L. B. JOHNSON, AND G. E. HOST. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37: 219–230.

SCHNEIDER, D. C. 2001. The rise of the concept of scale in ecology. BioScience 51:545–553.

STATZNER, B., J. A. GORE, AND V. H. RESH. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307–360.

STEINMAN, A., AND G. LAMBERTI. 1996. Biomass and pigments of benthic algae. Pages 295–313 *in* F. R. Hauer and G. A. Lamberti (editors). Stream ecology: field and laboratory exercises. Academic Press, Burlington, Massachusetts.

TAYLOR, B. W., A. R. MCINTOSH, AND B. L. PECKARSKY. 2002. Reach-scale manipulations show invertebrate grazers depress algal resources in streams. Limnology and Oceanography 47:893–899.

TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of North American Benthological Society 8:36–50.

TOWNSEND, C. R., S. DOLÉDEC, R. NORRIS, K. PEACOCK, AND C. ARBUCKLE. 2003. The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. Freshwater Biology 48:768–785.

TURNER, M. G., R. H. GARDNER, AND R. V. O'NEILL. 2001. Landscape ecology in theory and practice. Springer, Berlin, Germany.

WATERS, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology 43:316–320.

WELLNITZ, T. D., N. L. POFF, G. COSYLEÓN, AND B. STEURY. 2001. Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. Landscape Ecology 16:111–120.

WIENS, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

WIENS, J. A. 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47:501–515.

WOODWARD, G., AND A. G. HILDREW. 2002. Food web structure in riverine landscapes. Freshwater Biology 47:777–798.

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